A BIOGEOGRAPHIC ANALYSIS OF THE SEAWEED FLORA OF THE WEST COAST OF SOUTHERN AFRICA, FROM LÜDERITZ TO CAPE AGULHAS.

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Abstract

A biogeographic analysis of the seaweed flora of the area from Lüderitz to Cape Agulhas was undertaken. Biogeographic patterns were reviewed across 15 geographic regions. A TWINSPAN analysis showed a clear division of the area into two separate species communities. These two communities are the Benguela province, and the western overlap region between the Benguela and Agulhas provinces. The western overlap region was found to be the most diverse. Diversity was shown to decrease with a decrease in latitude. Patterns in endemism among the brown seaweeds follow this trend. In contrast to this, red and green endemics increase with an decrease in latitude. Shore distribution patterns were reviewed, and demonstrated an increase in diversity with a progression down the shore. Among the red seaweeds, this increase, with greater depth was considerable. Species distribution patterns in both shore and shore pool zones were found to follow the same pattern, except for a drop in species in the subtidal fringe pools, which this study concluded was a meaningless concept. These results have been reviewed in relation to present conservation areas along this shore, and future recommendations were made for location of sites for the conservation of seaweed. These were the formation of reserves between Lüderitz and Port Nolloth, between Yzerfontein and Melkbosstrand, and from Scarborough to Cape Hangklip. In some of these areas existing reserves need to make policy adjustments while in others reserves need to be established for the conservation of both diversity and uniqueness of seaweed species.

Introduction

Biodiversity, defined here as the variety and variability among living organisms and the ecological complexes in which they occur, and its conservation, have rapidly become an important issue on both scientific and political agendas (Noss 1990). This growing international concern for the conservation of biodiversity is evident when one considers the meetings, and conventions dedicated to the issue, such as the United Nations Convention on Biodiversity in 1992 (Wynberg 1992). Despite this new found concern there are areas where research into this conservation are lacking. Compared to terrestrial studies, research into marine biodiversity, and its conservation, is lagging, with particularly little attention being directed at algae. At the Convention of Biodiversity algae received no mention. The abundance and importance of algae is underestimated and as a result it has not played a significant role in the global biodiversity debate (Norton *et al.* 1996).

This long standing apathy towards seaweed biodiversity, as a global concern, is in many respects understandable. Seaweeds are notoriously difficult to describe, having few distinguishing features and a high degree of environmental plasticity (John 1994). With more extensive collections being made, and improved taxonomic methods providing better species lists this past trend is being reversed. Combined with the fact that approximately 70% of the earth's surface is comprised of salt water, and the growing apparent importance of seaweed in issues such as the global warming debate, ever increasing concern for the conservation of these organisms is being generated (Winston 1992).

A great deal of work needs to be done in order to remove the gap between marine and terrestrial ecology. A generous estimate is that 70% of marine algae of Africa have been described, indicating that we are far from knowing the true diversity of this continent (Winston 1992). Further more, an understanding of biodiversity does not end with a complete taxonomy of a group, but extends into an understanding of their biogeographic patterns (John & Lawson 1996). A knowledge of these patterns, and the driving forces behind them is essential if adequate conservation of any of these groups is to take place.

South African marine biogeography has a solid founding with a comprehensive survey carried out by Stephenson in the 1930s (Bolton 1986). Stephenson divided the coastline of South Africa into three distinct marine provinces: the cold-temperate province on the west coast, the warm-temperate province on the south coast, and the sub-tropical province on the east coast, known now as portions of the Benguela, Agulhas and Indo-Pacific provinces respectively (Bolton 1986; Lüning 1990). While Stephenson's work was confined to South Africa, the extent of these provinces is not. The focus of this project is on the seaweed biogeography of a portion of the Benguela province which in entirety stretches from Mossamedes in Angola to Cape Agulhas. This province is different to other cold-temperate regions in its temperature regime, and there is much debate with regard to its truly being a cold-temperate region, and is presently being referred to as a cool-temperate region (Bolton & Anderson in press).

The long geographic isolation of the southern African coastline makes for an interesting, and in many ways unique seaweed flora (South 1979). Conditions prevailing along the west coast today, which encompass cool upwelling as a result of offshore winds, combined with El nino-Southern Oscillation (ENSO) events make this flora distinct. The west coast has unusual combinations of species as well as high levels of endemism (Hommersand 1986). The seaweed flora of the cool-temperate region of southern Africa is in this way, and many others different to that of other temperate regions, making this area of particular biogeographic interest and conservation importance.

Compared to other areas of the world, the coastline of South Africa is still relatively pristine (Robinson & de Graaf 1994). Therefore it is a crucial time to address which areas of the coast would be most effective for the conservation of our seaweed before the onset of any environmental degradation. It may be that we have the opportunity to conserve species which are threatened elsewhere. Recent political changes may enforce the review of coastal management practices and legislation, thereby creating opportunities for the incorporation of seaweed into marine reserve design and location. The economic significance of the coasts of Southern Africa will only grow, from both a tourism and industry point of view. Seaweed conservation needs to be reviewed in the light of the potential of seaweed industries to expand (Levitt *et al.* 1995). Considering these facts, a biogeographic analysis of this region should be significant, and well timed.

The selection of marine reserves in South Africa has in the past have been based on local community concern, rather than on scientific principles. There is a move towards finding the conservation value of the coast of South Africa, based on more scientific principles (Emanuel 1992). To ensure the successful conservation of the South Africa's coasts, Hockey and Buxton (1989) recognise the need for appropriate research from which guidelines for the sizing and spacing of marine reserves can be established. For this to be achieved in a holistic manner, the inclusion of seaweed in any plan for coastal conservation is essential.

This project is a contribution to a biogeographic understanding of the phycological patterns displayed in a portion of the Benguela province from southern Namibia and the western overlap region with the Agulhas province. This has been done so as to facilitate future studies into possible conservation plans for this stretch of the coastline.

Methods

Study Site and Material

The biogeographic area considered in this project is from Lüderitz in southern Namibia (26° 40' S; 16° 10' E) to Cape Agulhas (34° 55' S; 20° 05' E). This study area includes a portion of the cool-temperate Benguela Province, and the western overlap region where the Benguela and warm-temperate Agulhas provinces meet (Lüning 1990, Bolton & Anderson in press). Temperature is considered to be the primary determining factor accounting for species distribution. The cool-temperate Benguela province is characterised by the cold Benguela current and seasonal upwelling, which causes rapid temperature changes (Lüning 1990). Mean annual temperatures range from 12° - 16°C. Between these two provinces lies the western overlap region, this being situated between Cape Point and Cape Agulhas, exhibiting intermediate temperatures, being warmer than the cool Benguela province and cooler than the warm Agulhas province (Bolton & Anderson in press). False Bay, falling within this region, has somewhat higher temperatures due to its enclosed nature as a bay (Bolton 1986). A further important result of the upwelling regime on the west coast is the resultant increased nutrient status of the water (Hommersand 1986).

Only macrophytic seaweed species were considered in this project. The distributional data, their endemic status to southern Africa, shore zone distribution and substratum preference data were extracted from *Seaweeds of the South African West Coast* (Stegenga *et al.* in press). This data includes seaweeds of the divisions Rhodophyta, Chlorophyta and Phaeophyta, in this project also referred to as the reds, greens and browns respectively. Excluded from the data are the non-geniculate coralline red algae. In addition to this, Lawson et al's (1991) lists of the flora of Namibia were used, but only to ascertain the presence of those species previously mentioned in Stegenga et al's (in press) document whose distributions beyond the northern Cape were uncertain. These two documents provided the necessary information needed in carrying out a biogeographic analysis.

The study area was divided into fifteen geographic regions of varying size (see fig 1). The classification of regions were based on a knowledge of the coastline, where for example the Cape Peninsula has been divided into smaller areas to detect more closely the point of transition into the western overlap region. The smallest region, from Kommetjie to Scarborough, is based on Stephenson's suggestion that this region formed the junction between the west coast and the western overlap region. Species were recorded in these geographic regions on a presence absence basis. When species were recorded in discontinuous areas, with two or less geographic regions between them, their distribution was assumed to be continuous, merely not recorded in those regions due to poor collections. In cases where disjunctions were clearly of environmental significance, such as in the case of estuarine or lagoon species, discontinuities were left unaltered.

Table 1 The geographical regions chosen for study in this project.

Region	Geographical location	Approximate distance of coast (km)
1	150 km to the north of Lüderitz	150
2	Lüderitz to Port Nolloth	330
3	Port Nolloth to Hondeklipbaai	120
4	Hondeklipbaai to Lamberts Bay	210
5	Lamberts Bay to Saldanha	150
6	Saldanha to Yzerfontien	40
7	Yzerfontien to Melkbosstrand	50
8	Melkbosstrand to Kommetjie	55
9	Kommetjie to Scarborough	7.5
10	Scarborough to Smitswinkelbaai	30
11	Smitswinkelbaai to Muizenberg	20
12	Muizenberg to Cape Hangklip	55
13	Cape Hangklip to Hermanus	45
14	Hermanus to Cape Agulhas	95
15	Cape Agulhas and 150 km to the east	150

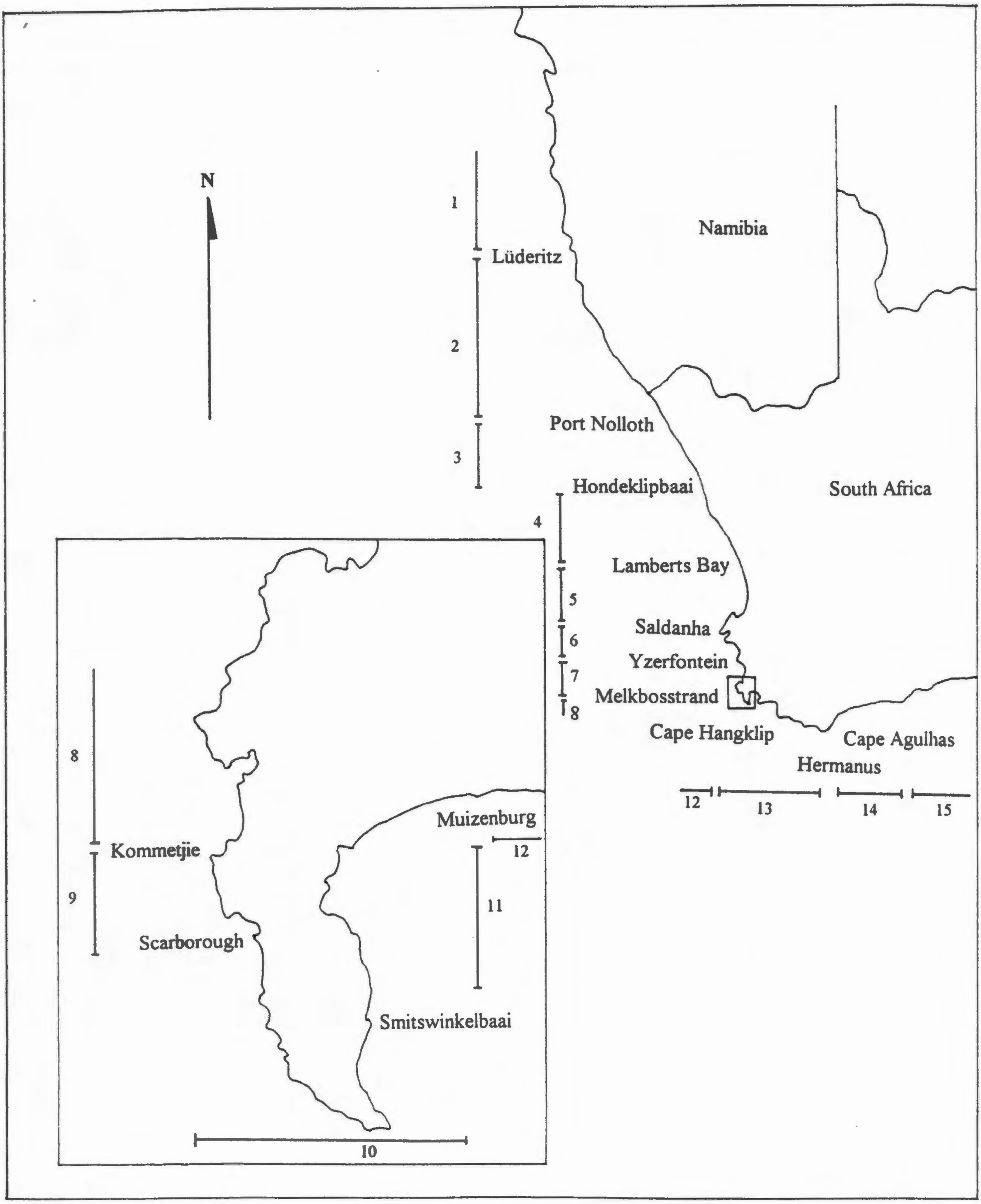

Fig 1 The study area, depicting the west coast of South Africa and southern Namibia and the western overlap region towards the Agulhas province, with the fifteen geographic regions indicated. The Cape Peninsula is inset.

Methods

The two main themes of this biogeographic analysis are firstly the biogeographic distribution patterns, and secondly shore habitat distribution patterns.

Biogeographic distribution patterns.

The presence or absence of each species in the fifteen selected geographic regions, and simultaneously, the its endemic status to southern Africa, were recorded. The fifteen regions were then compared graphically from the point of view of both diversity, looking at species numbers and divisions, and uniqueness, where endemism and species turnover were reviewed.

A two-way indicator species analysis (TWINSPAN) computer programme was used to provide a classification of the seaweed floras of the region. This is done by progressive splitting of ordinations, based on species composition. In this way the coastline may be divided broadly into communities based on differing groups of species.

Beta diversity was determined to establish the rates of species turnover between adjacent geographical regions. For this purpose the regions were grouped into comparison sites. The Beta diversity (**B**) values between each adjacent zone were calculated according to the method of Wilson and Shmida (1984) (see formula a). A **B** value of 0 indicates no change, while 1 represents complete turnover. These were then represented graphically.

a) $\mathbf{B} = (\mathbf{g_E} + \mathbf{l_E}) / 2\mathbf{S}$

Where **B** = Beta Diversity

$\mathbf{g_E}$ = Number of species gained along gradient E

$\mathbf{l_E}$ = Number of species lost along gradient E

S = Mean sample richness along gradient

In addition to this the numbers of species gained, lost and in common between each comparison region were calculated and graphed. This was done in order to be able to attribute the changes in Beta diversity between each geographical comparison region to either species losses or gains.

Shore habitat diversity.

Seaweed shore communities are characterised by vertical zonation as a result of variable biotic and abiotic factors along this gradient. In this study the shore was divided into seven vertical zones (see table 2), using the classical zone classification as described by Lüning (1990), into which species were recorded on a presence or absence basis. These zones were then broken into those areas of rocky shore, in this case simply termed shore zones, and those with tidal pools, termed shore pool zones. These shore zones and shore pool zones are as follows:

Table 2 Shore zones.

Zone number	Shore Zones	Shore Pool zones
1	Supralittoral	Supralittoral pools
2	Upper-eulittoral	Upper-eulittoral pools
3	Mid-eulittoral	Mid-eulittoral pools
4	Lower-eulittoral	Lower-eulittoral pools
5	Subtidal fringe	Subtidal fringe pools
6	Shallow-sublittoral	-
7	Deep-sublittoral	-

Substratum preferences, broken broadly into those species which are epilithic, growing attached to shore, or epiphytic and epizoic, attached to plants and animals respectively (broadly classed together for the purpose of this study as epibiotic), and those seaweeds which grow on both epibiotic and epilithic substratum, were recorded. The different habitats were then examined for patterns, from both a uniqueness vantage point, looking at endemism and as well as that of diversity, in terms of both species numbers, the contribution of each division, and different substratum preferences.

Finally the results were considered from a conservation perspective, comparing those areas best designated for seaweed conservation with those areas presently declared reserves along this coast, again taking into consideration both uniqueness and representativeness.

Results

Biogeographic distribution patterns.

The total number of species recorded around the coast from southern Namibia at Lüderitz to Cape Agulhas was 388. Of the geographic regions, region 11, from Smitswinkelbaai to Muizenberg is the most diverse with 277 species recorded (see table 3).

Table 3 Total species numbers recorded in each geographic region.

Region number	Geographic region	Species numbers in each region
1	150 km north of Lüderitz	116
2	Lüderitz to Port Nolloth	126
3	Port Nolloth to Hondeklipbaai	142
4	Hondeklipbaai to Lamberts Bay	149
5	Lamberts Bay to Saldanha	164
6	Saldanha to Yzerfontein	183
7	Yzerfontein to Melkbosstrand	180
8	Melkbosstrand to Kommetjie	213
9	Kommetjie to Scarborough	204
10	Scarborough to Smitswinkelbaai	231
11	Smitswinkelbaai to Muizenberg	277
12	Muizenberg to Cape Hangklip	265
13	Cape Hangklip to Hermanus	240
14	Hermanus to Cape Agulhas	234
15	Cape Agulhas and 150 km eastwards	210

The number of species from each division at the various geographic regions shows the Chlorophyta and Phaeophyta to have their greatest number of species from Smitswinkelbaai to Muizenberg (region 11), on the western side of False Bay. The Rhodophyta, reds peak in the adjacent region from Muizenberg to Cape Hangklip (region 12), on the eastern side of False Bay. The general pattern of an increase in species around the Cape Peninsula, with a decline both to the east, and more particularly to the north, is a trend followed by all three of the divisions (see fig 2)

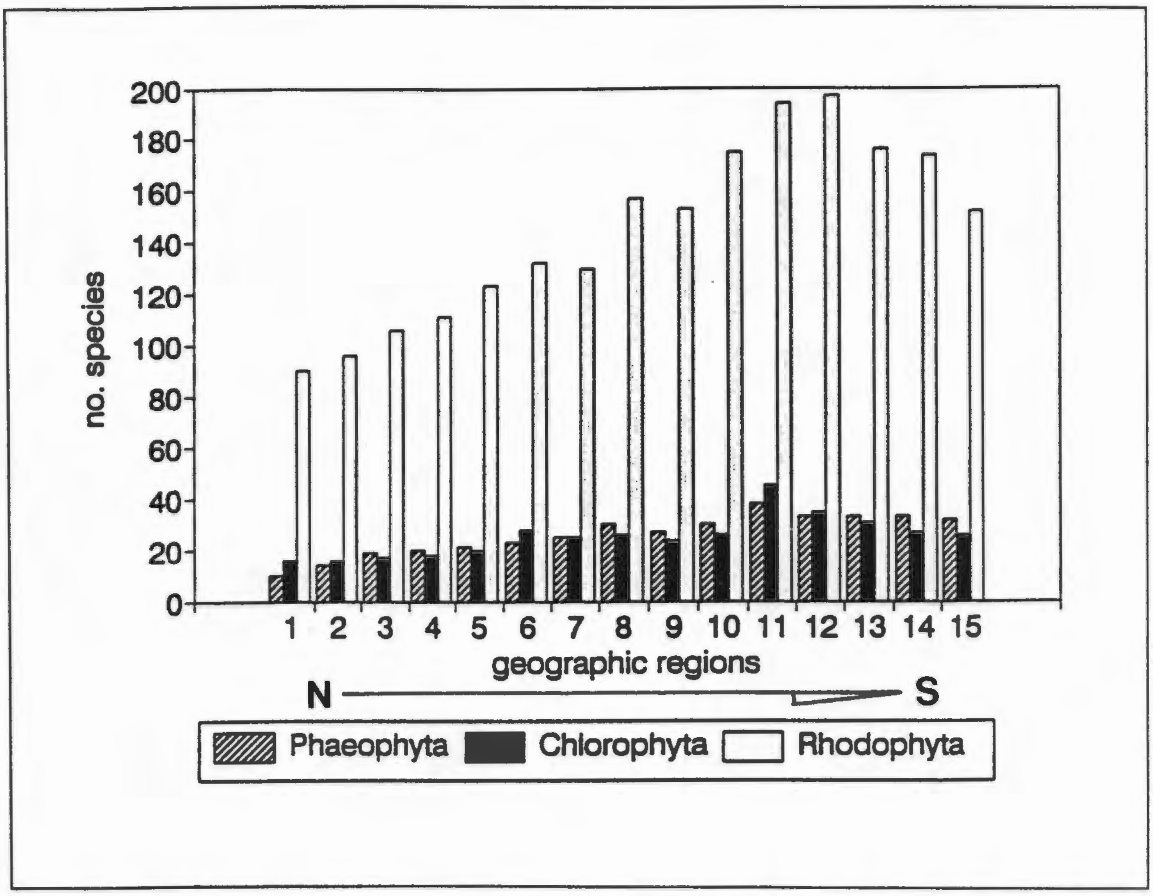

Fig 2 The number of species from each division at each geographic region (for geographic regions see table 2 & fig 1).

Across the entire study site the browns contribute 14%, the greens 15%, and the reds 71% to the total flora. This proportion of the divisions remains fairly constant throughout the study site (see fig 2). There is a marginal increase in Chlorophyta both in the Smitswinkelbaai to Muizenberg area (region 11), and between Saldanha and Yzerfontein (region 6). Around the Peninsula this slight increase is reflected in a dip in the percentage of Rhodophyta (see fig 3).

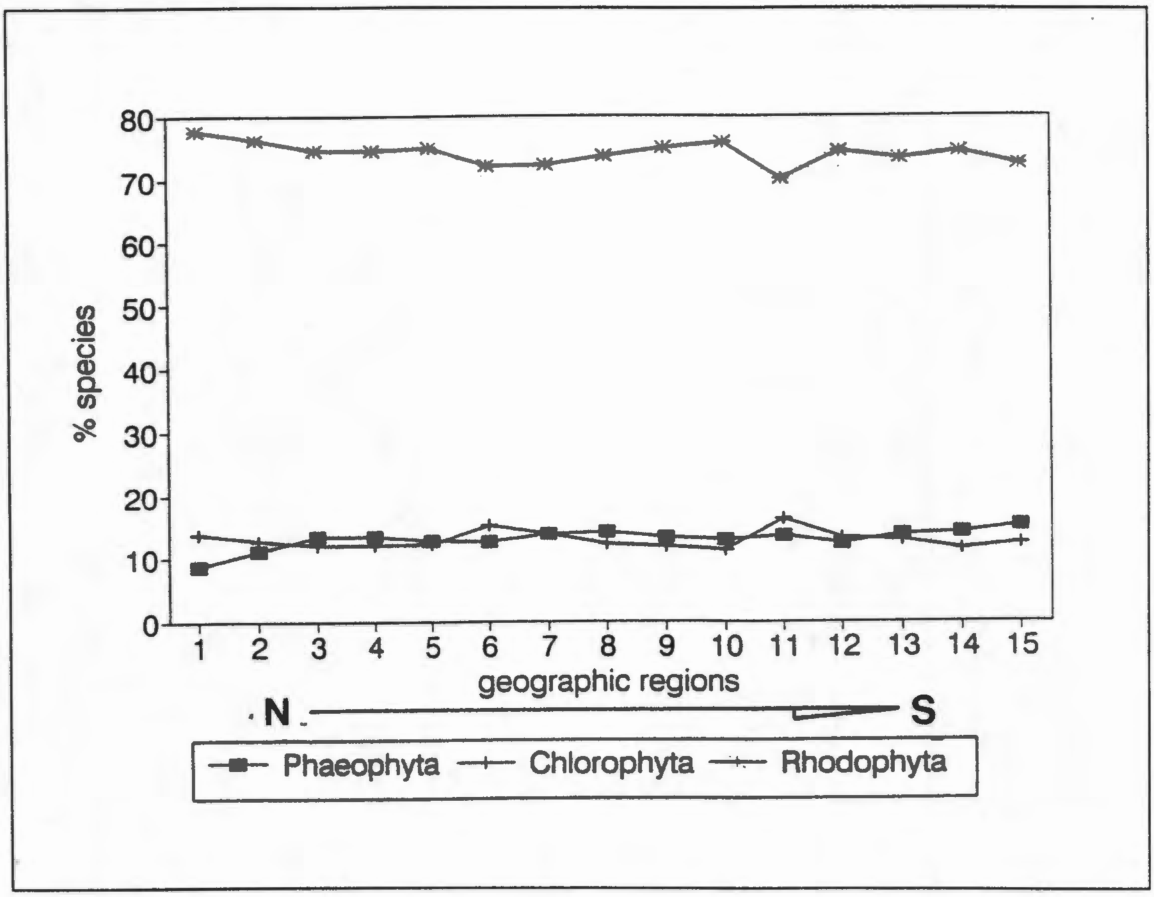

Fig 3 The percentage from each division at each geographic region (for geographic regions see table 2 & fig 1).

Beta diversity figures show the greatest turnover of species to be between the comparison regions from Scarborough, around the Cape Peninsula to the Smitswinkelbaai to Muizenberg region (comparison regions 10 & 11). This turnover point, the greatest on this stretch of coast, is of a 0.3 magnitude, indicating a turnover of one third of the species. These regions also account for the smallest area of the shoreline, together covering approximately 60 km (see table 1). A second peak in turnover is evident between comparison regions Yzerfontein to Melkbosstrand and Melkbosstrand to Kommetjie (comparison regions 7 & 8). A third site of turnover, similar in magnitude, is between the regions of Lüderitz to Port Nolloth (Comparison regions 1 & 2) (see fig 4).

Table 4 A legend of the comparison numbers for the various regions compared.

Comparison number	Regions compared
1	1 & 2
2	2 & 3
3	3 & 4
4	4 & 5
5	5 & 6
6	6 & 7
7	7 & 8
8	8 & 9
9	9 & 10
10	10 & 11
11	11 & 12
12	12 & 13
13	13 & 14
14	14 & 15

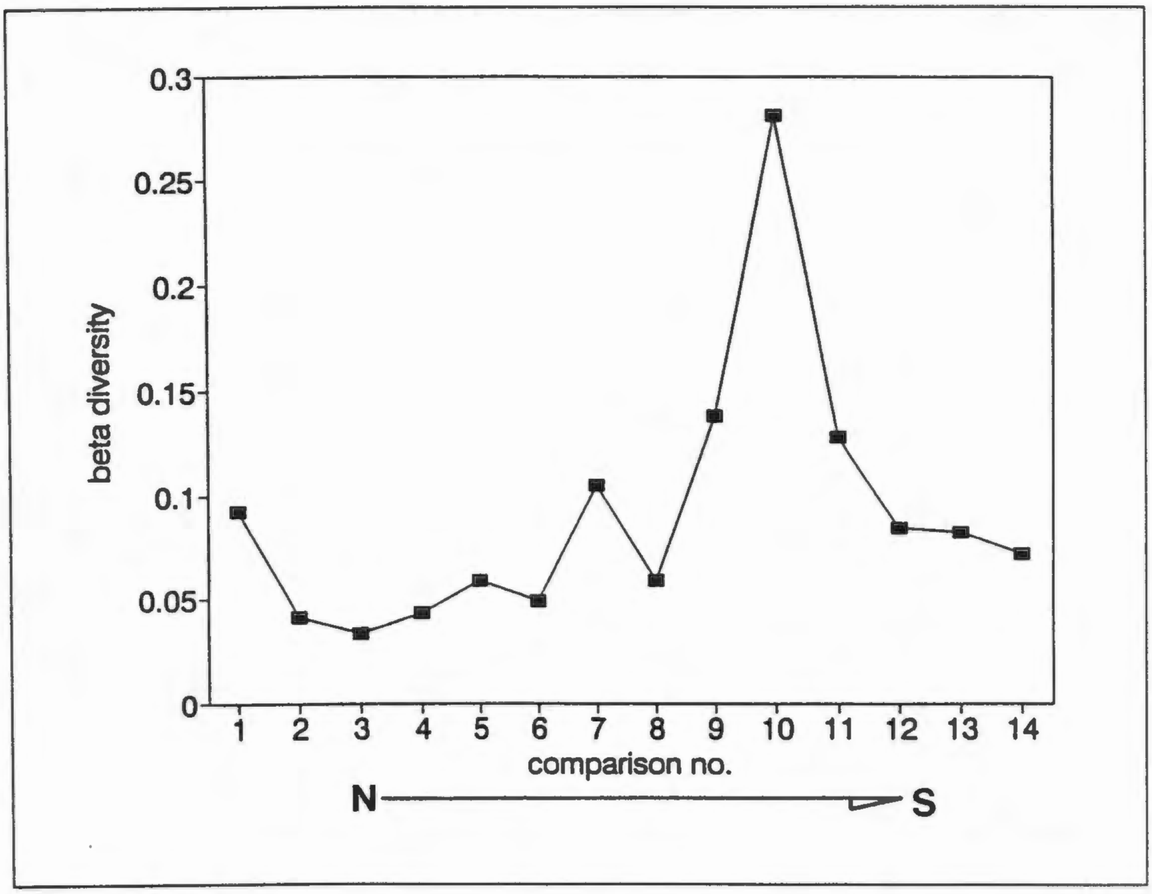

Fig 4 Change in beta diversity between adjacent areas from north of Lüderitz to east of Cape Agulhas (see table 4 for areas of comparison).

Figure 5 demonstrates whether this turnover is a function of species being lost, or gained. There is a progressive loss and simultaneous gain of species from Yzerfontien to Melkbosstrand (region 7) towards the south east. Within this general pattern we see specific sites of high turnover, the greatest loss and gain at comparison region 10, around the Cape Peninsula from the region of Scarborough, to Smitswinkelbaai, to Muizenberg. Comparison regions 1, from north of Lüderitz to Port Nolloth and region 7 from Yzerfontein to Kommetjie both have high gains of species. Regions 1 also has a high portion of species lost, as does region 6 from Saldanha to Melkbosstrand (see fig 5).

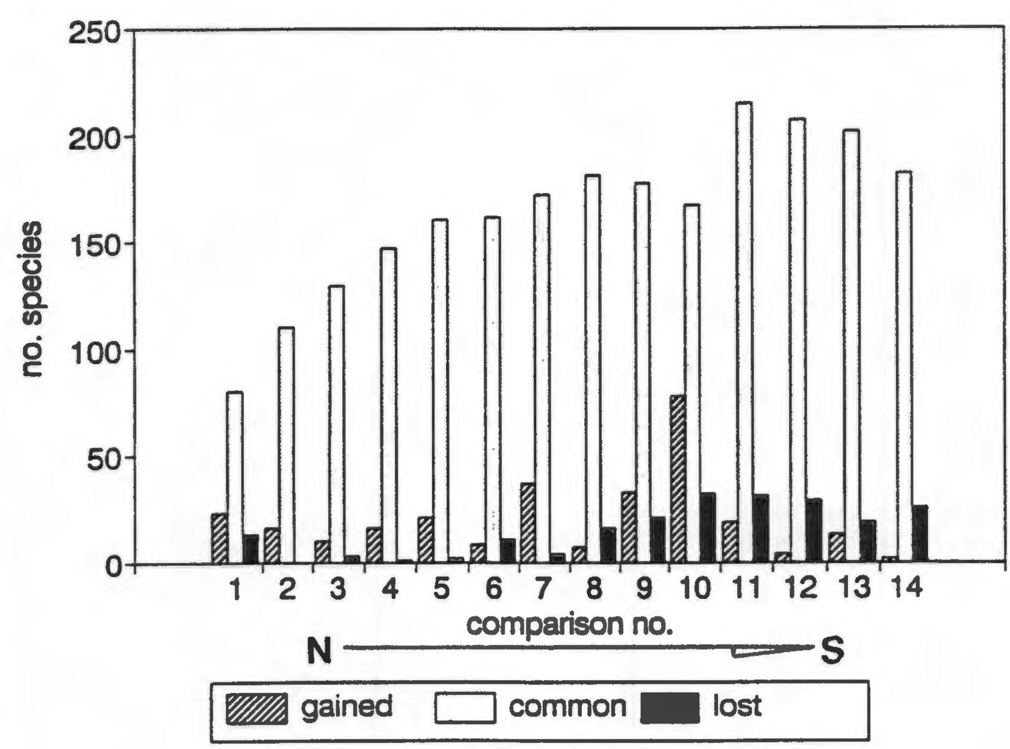

Fig 5 The number of species lost, in common and gained between adjacent areas moving from north of Lüderitz to east of Cape Agulhas (see table 4 for areas of comparison).

The results of the TWINSPAN analysis show the study area to be broken into two main regions, this separation occurring on the Cape Peninsula, at Smitswinkelbaai (region 10), dividing the area into a north westerly region and an easterly region. Each region is in turn divided again into two regions. On the south east coast the area is divided into False Bay (regions 11 & 12) and east of False Bay (regions 13, 14 & 15). The two main divisions on the west coast are the regions from Smitswinkelbaai (region 10) north west to Melkbosstrand (region 8), and from Melkbosstrand to southern Namibia (region 1). This second split on the west coast from Melkbosstrand to southern Namibia is further divided into two areas. These two areas are from Yzerfontein (region 7) to Lamberts Bay (region 4), and to the north from Hondeklipbaai (region 3) to southern Namibia (region 1) (see fig 6).

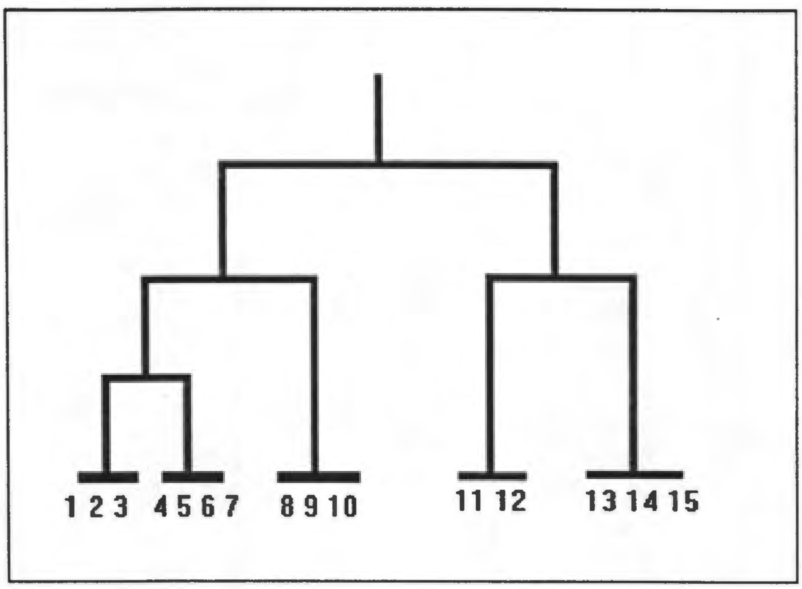

Fig 6 Dendogram of results of a TWINSPAN analysis of areas 1 to 15 (for geographic regions see table 1).

The total number of southern African endemics found along the southern Namibian and South African west coast, and the western overlap region is 197, which is 50.7% of the total species found in this region. The number of endemics in each region follows closely the number of species found in that region (see fig 7).

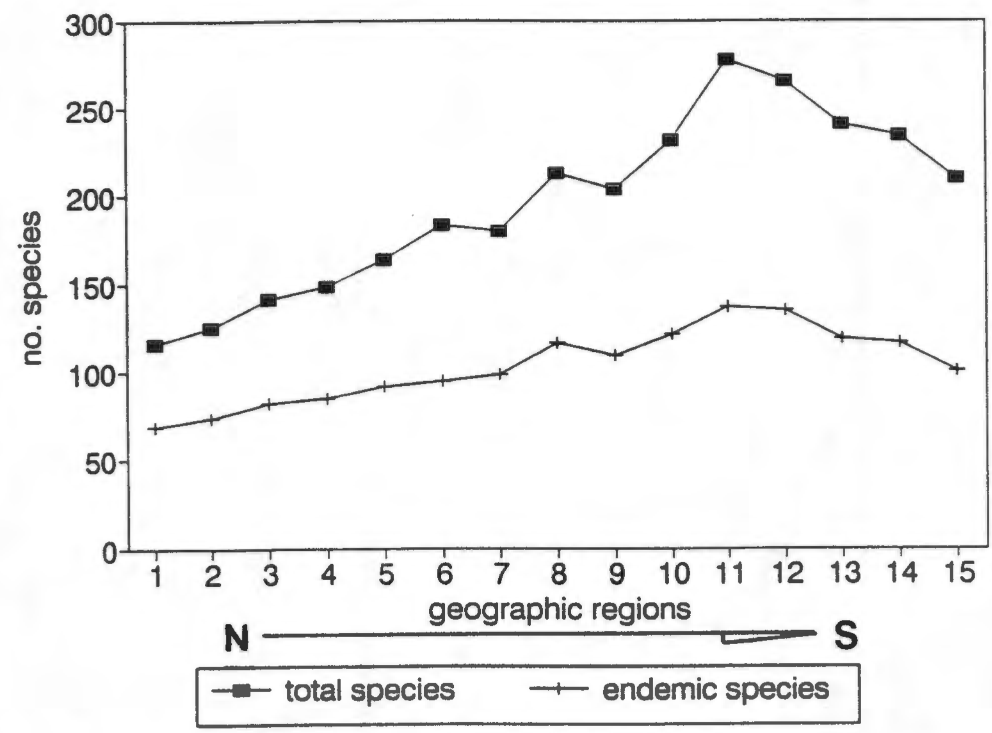

Fig 7 The total number of southern African endemic species at each geographic region in relation to the number of species found in that region.

The total percentage of endemics found in each region decreases with a southerly progression from 60% north of Lüderitz, to 48% at Cape Agulhas (see fig 8). Within this trend two dips in endemism occur between the geographic region 6, which is Saldanha Bay, and region 11, which is the Smitswinkelbaai and Muizenberg region, covering the western side of False Bay.

The percentage endemism of the red algae in each geographic region drops in a shallow slope to the south, going from 70% to 60%. The greens also drop to the south, though less steadily, with few endemics in the far north west, rising to 65% in the northern Cape and dropping to 35% in the False Bay area. In contrast to this pattern of a decrease in the percentage of endemics in each division in each region, the browns show a steady increase to the south and south east. The increase in brown endemics is relatively steep, going from less than 10% in the north to just less than

40% in the south. The high numbers of reds, which subsequently contribute more to the total endemics, accounts for a major portion of the total percentage of southern African endemics in each geographic region, this curve therefore, closely following that of the percentage of reds which are endemic (see fig 8).

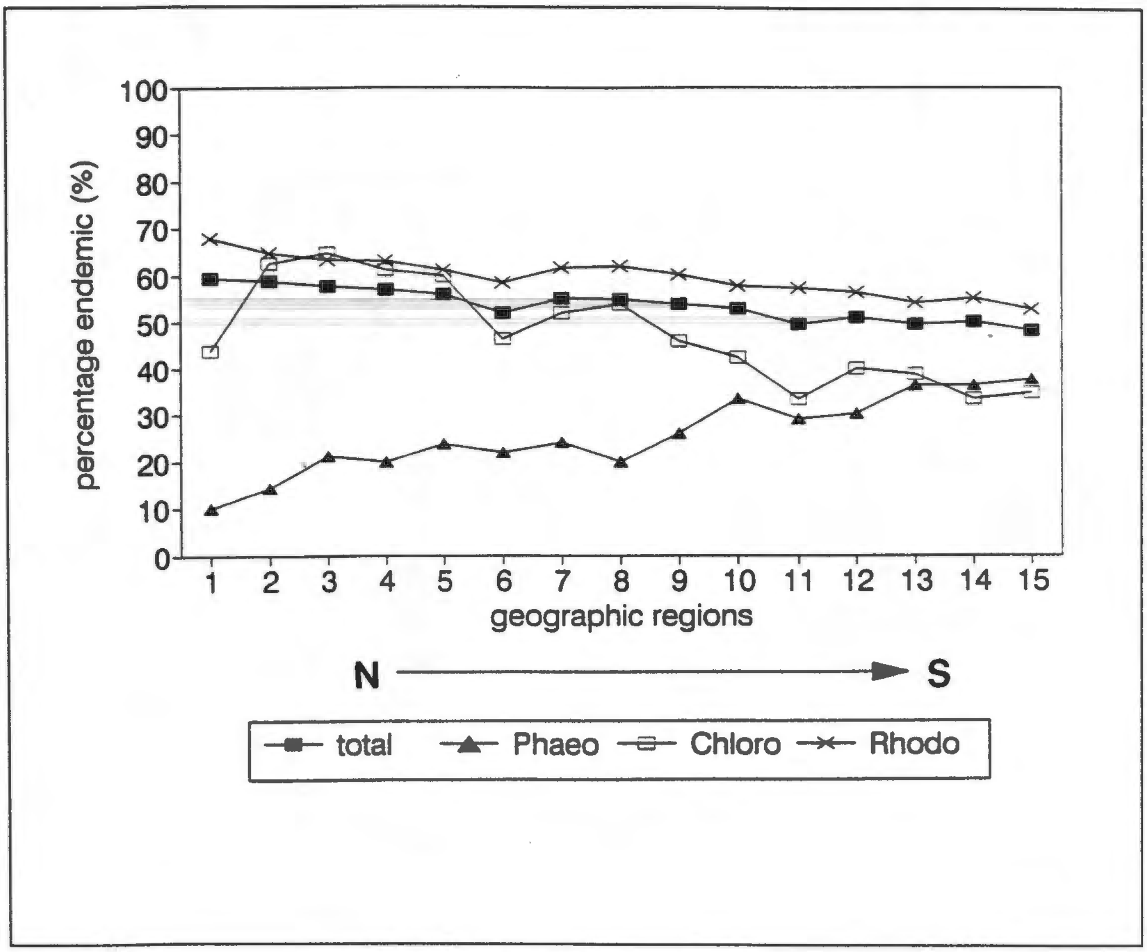

Fig 8 The percentage of southern African endemics of the total seaweed flora at each geographic region, and the percentage of endemics of each division at each region.

The number of endemics in each shore zone follows a similar pattern to the increase in the numbers of species in each shore zone. There is a progression from the supralittoral and upper-eulittoral which have a small proportion of endemics, through the mid- and lower-eulittoral where the proportions are high, with almost half of the subtidal fringe being comprised of endemics, and while increasing in number in the shallow and deep subtidal, the proportion declines (see fig 9).

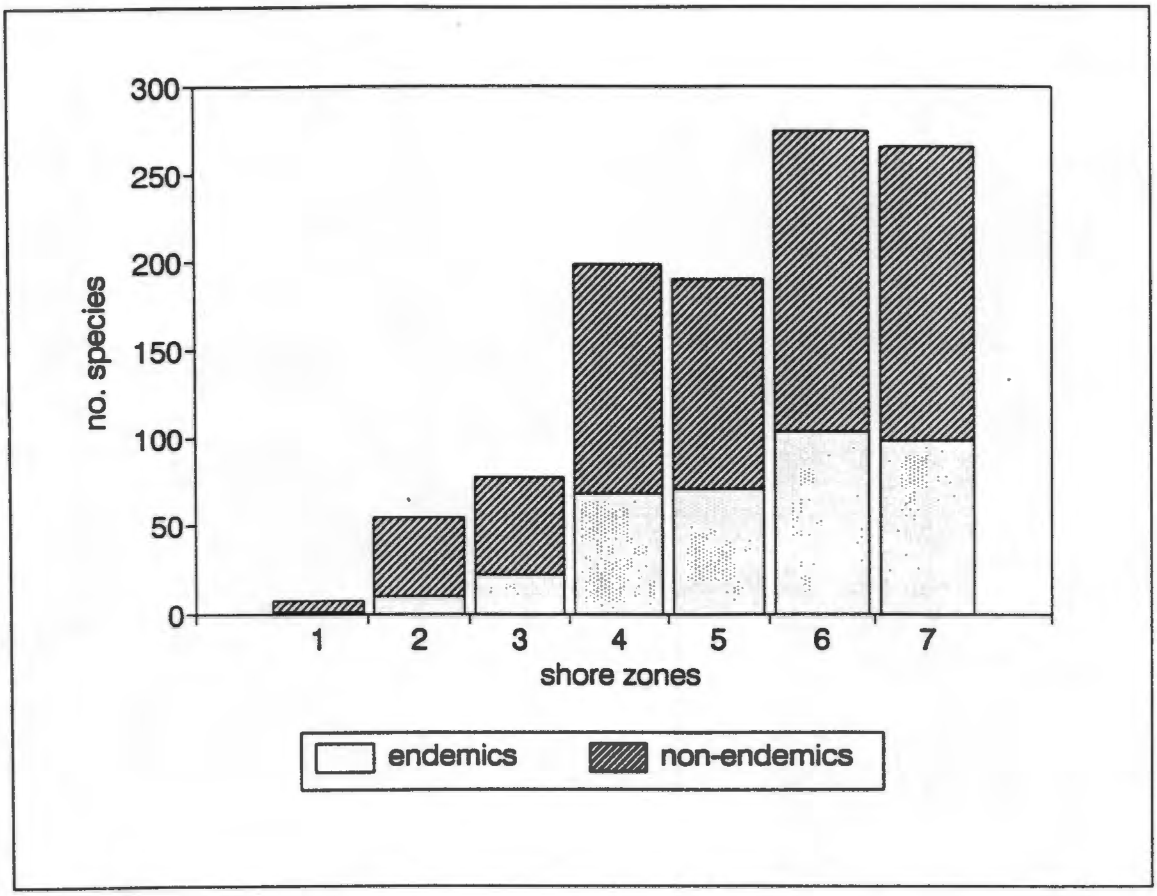

Fig 9 The number of endemics in each shore zone in relation to the number of species found in that zone (for shore zone descriptions see table 2).

The proportion of endemism in the shore pool zones also follows closely the number of species in each shore pool zone, accounting for approximately one third of the seaweeds in each shore pool zone. The exception to this is shore pool zone 1 which has only one endemic, *Polysiphonia incompta*, contributing only ten percent to the total flora (see fig 10).

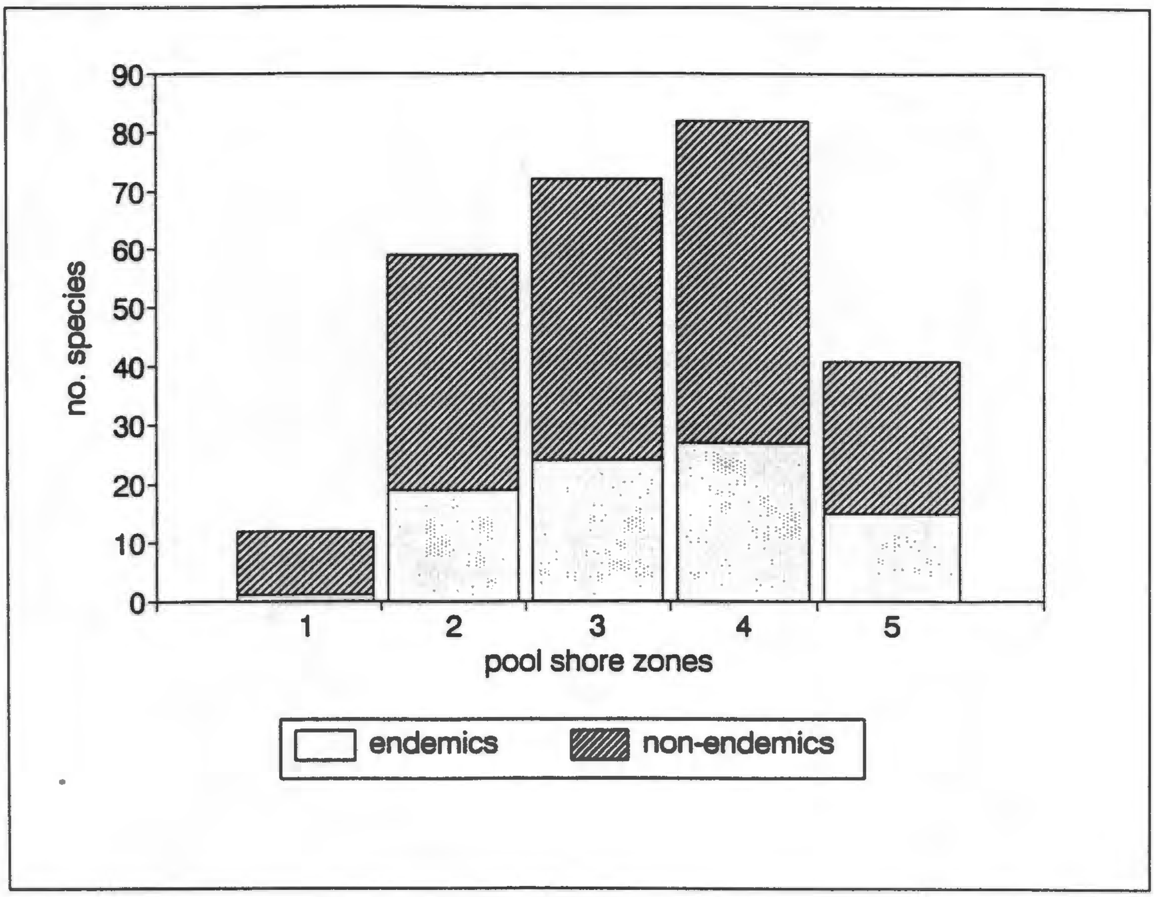

Fig 10 The number of endemics in each shore pool zone in relation to the number of species found in that zone (for shore pool zone descriptions see table 2).

Shore habitat diversity.

Seaweed diversity increases with a vertical progression down the shore. The most diverse zone in the shallow sublittoral (zone 6). The greatest number of Chlorophyta are found in the lower eulittoral (zone 4), and the greatest number Phaeophyta in the shallow sub-littoral (zone 6). Rhodophyta numbers almost triple between the mid-eulittoral (zone 3) and the lower-eulittoral (zone 4), they are most abundant in the lower eulittoral (zone 7) (see fig 11).

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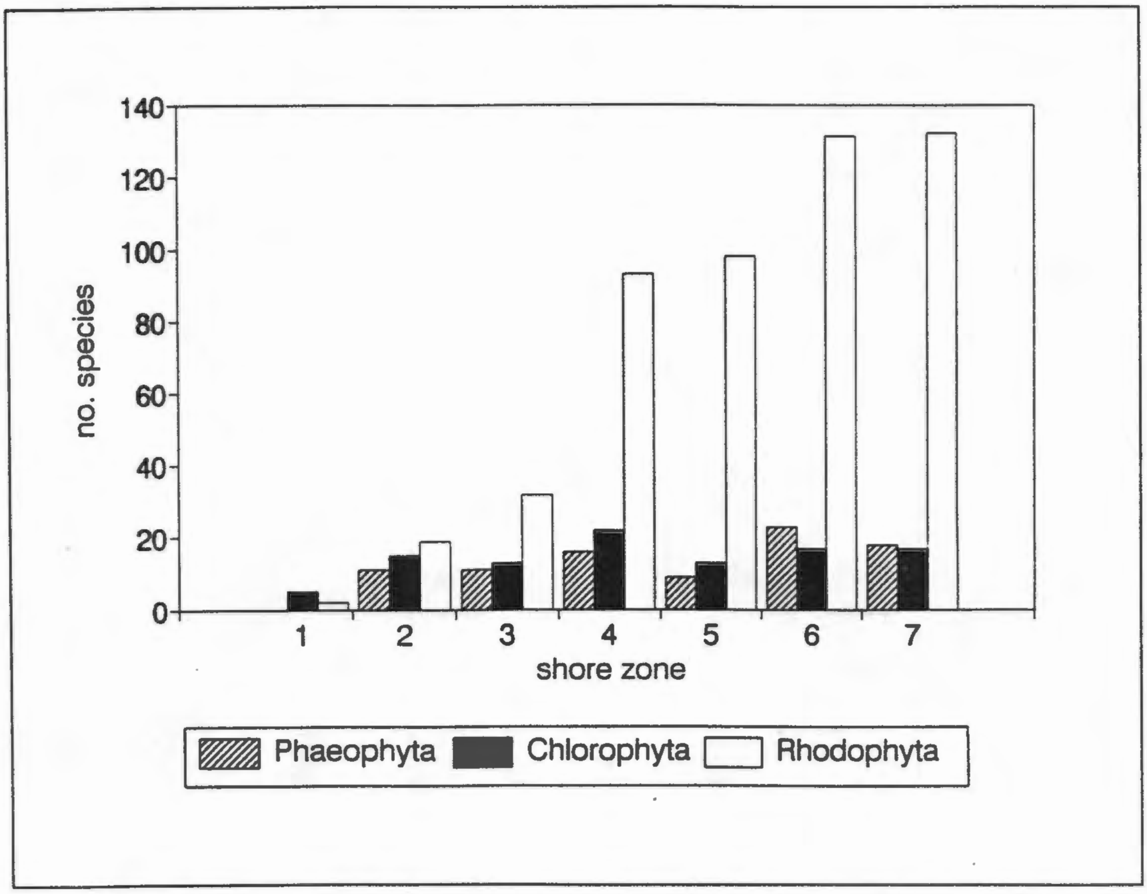

Fig 11 The number of species of each division found in each shore zone (for shore zone descriptions see table 2).

The Rhodophyta show a progressive increase in percentage of species present in each shore zone with increased submersion, accounting for 80% of the species in the deep sub-littoral (zone 7), and only 30% in the supralittoral (zone 1). The Chlorophyta are dominant in the supralittoral contributing around 70%, and declining to just over 10 % in the deep sub-littoral. The Phaeophyta are absent from the supralittoral, and show a gradual decline from the upper-eulittoral (zone 2) where they account for approximately 25% of the flora, to the deep sub-littoral where they constitute around 15%. They show a slight increase in the shallow sub-littoral (zone 6) relative to the deep sub-littoral and the subtidal fringe (zone 5) (see fig 12).

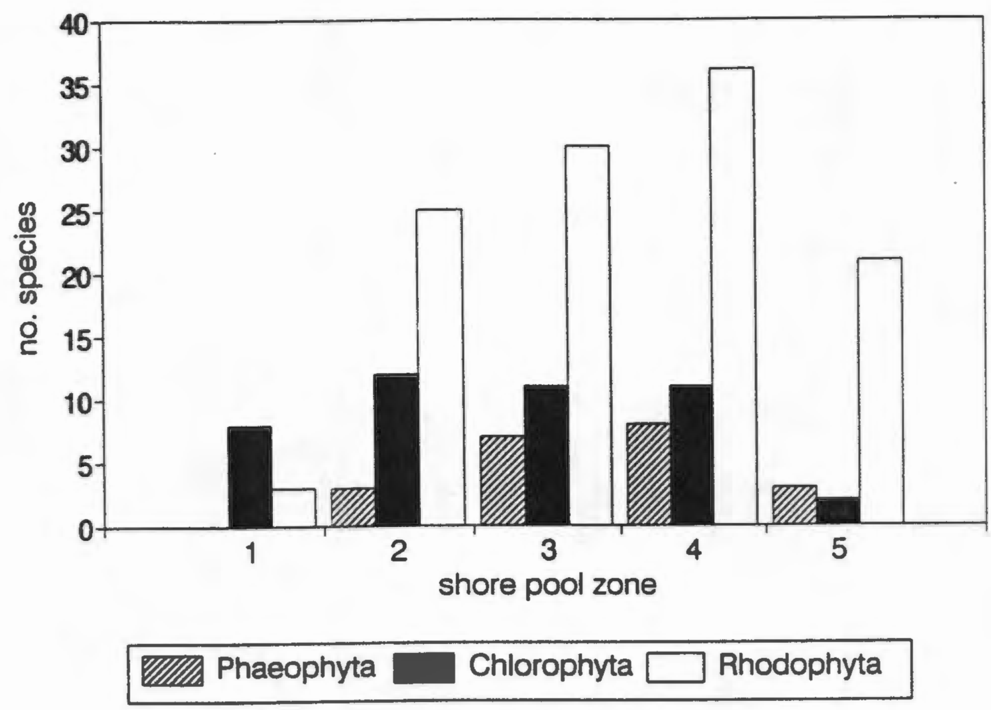

Fig 12 The number of species from each division in each shore pool zone (for shore pool zone descriptions see table 2).

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The percentage of seaweed of the total flora found in each shore pool zone decreases with an increase in submersion, with a vertical progression down the shore. In the supralittoral shore pool zone 61% of the seaweeds are found in pools, 47% in the upper eulittoral, 46% in the mid-eulittoral, 30% in the lower eulittoral and 18% in the subtidal fringe. The number of species found in each pool shore zone also increases with a vertical progression down the shore. There is a decrease in species in the pools of the subtidal fringe (zone 5) (see fig 13).

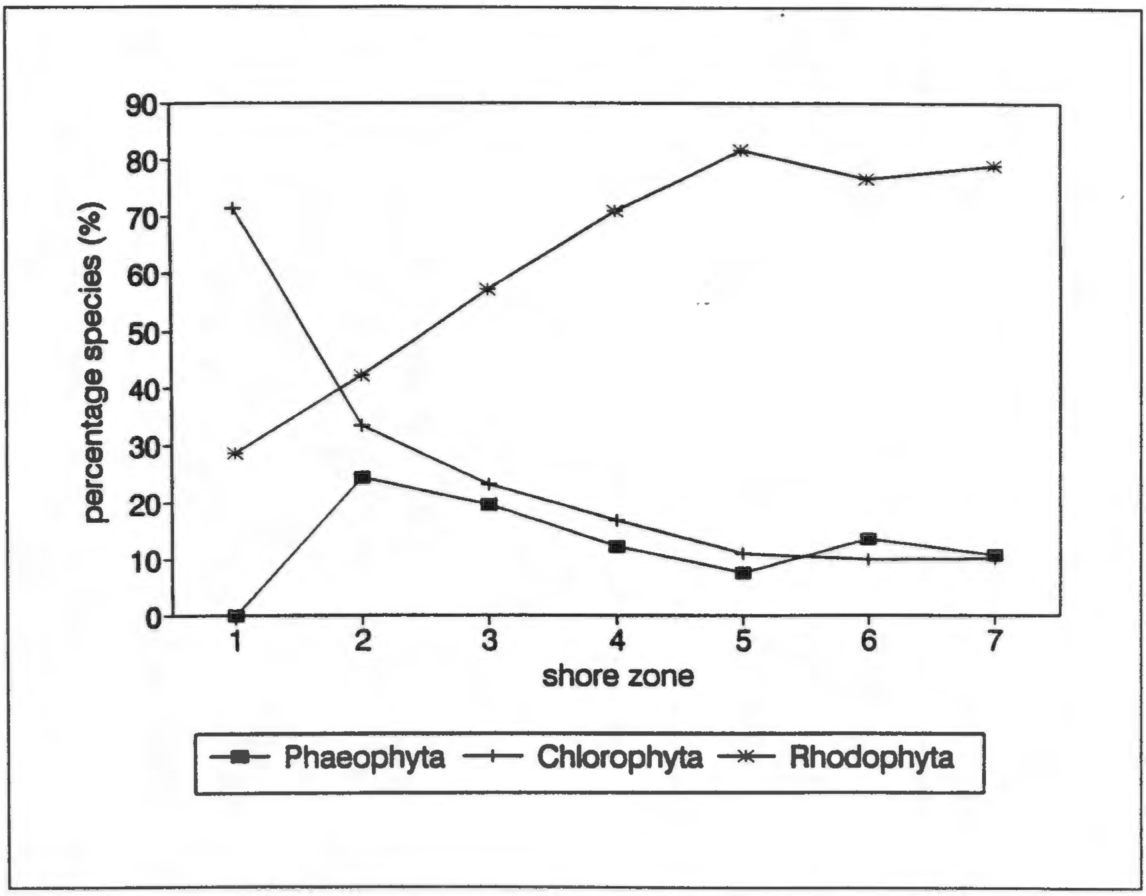

Fig 13 The percentage of species of each division found in each shore zone (for shore zone descriptions see table 2).

The percentage of each division found in each pool shore zone to a large extent mirrors that of the shore zones (see fig 12 & 14). While the pattern stays the same, the actual percentages differ to some extent. In the upper eulittoral (zone 2) more than 60% of the species are Rhodophyta and less than 10% are Phaeophyta (see fig 14).

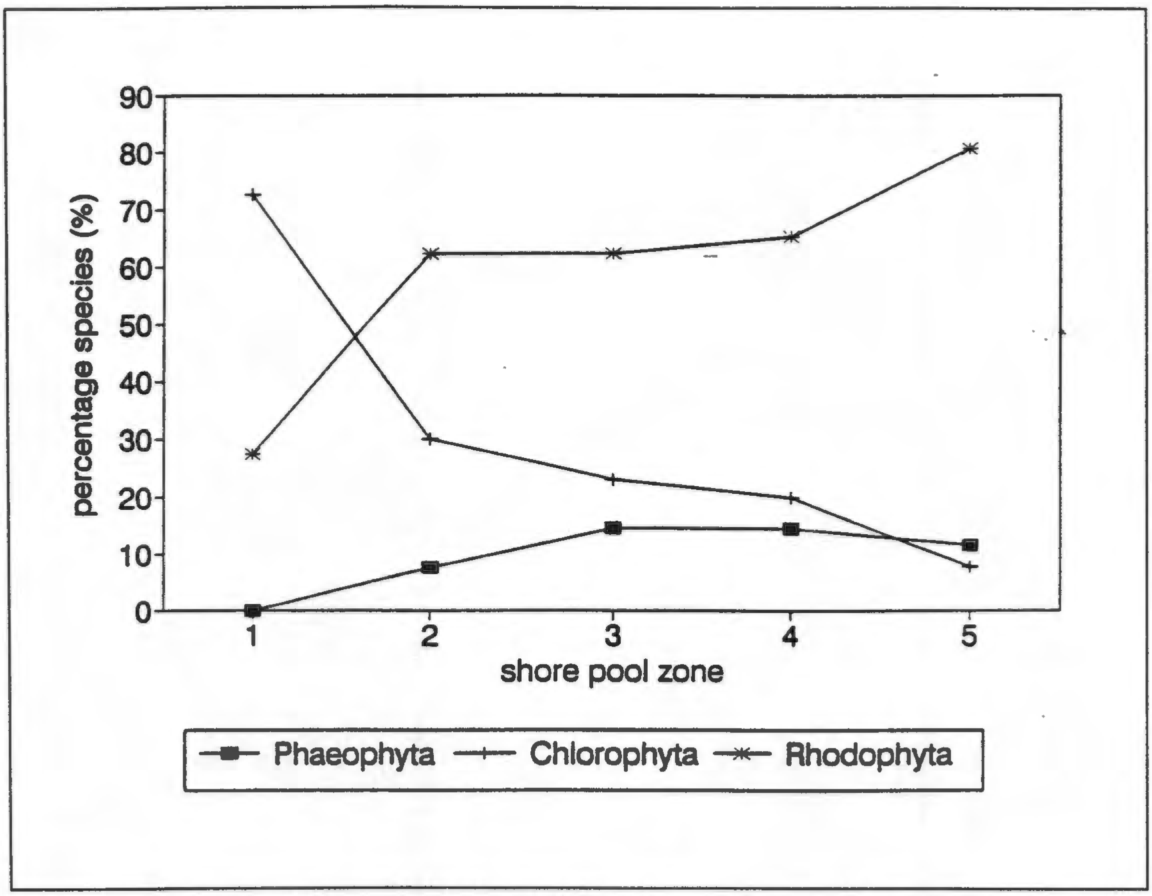

Fig 14 The percentage of species from each division found at each pool shore zone (for shore pool zone descriptions see table 2).

The majority of the seaweed flora are epilithic, followed by epibiotic species and to a lesser extent species that are both epilithic and epibiotic. These three relationships remain fairly constant over the geographic regions, as demonstrated by the percentage each contributes to the total flora (see fig 15).

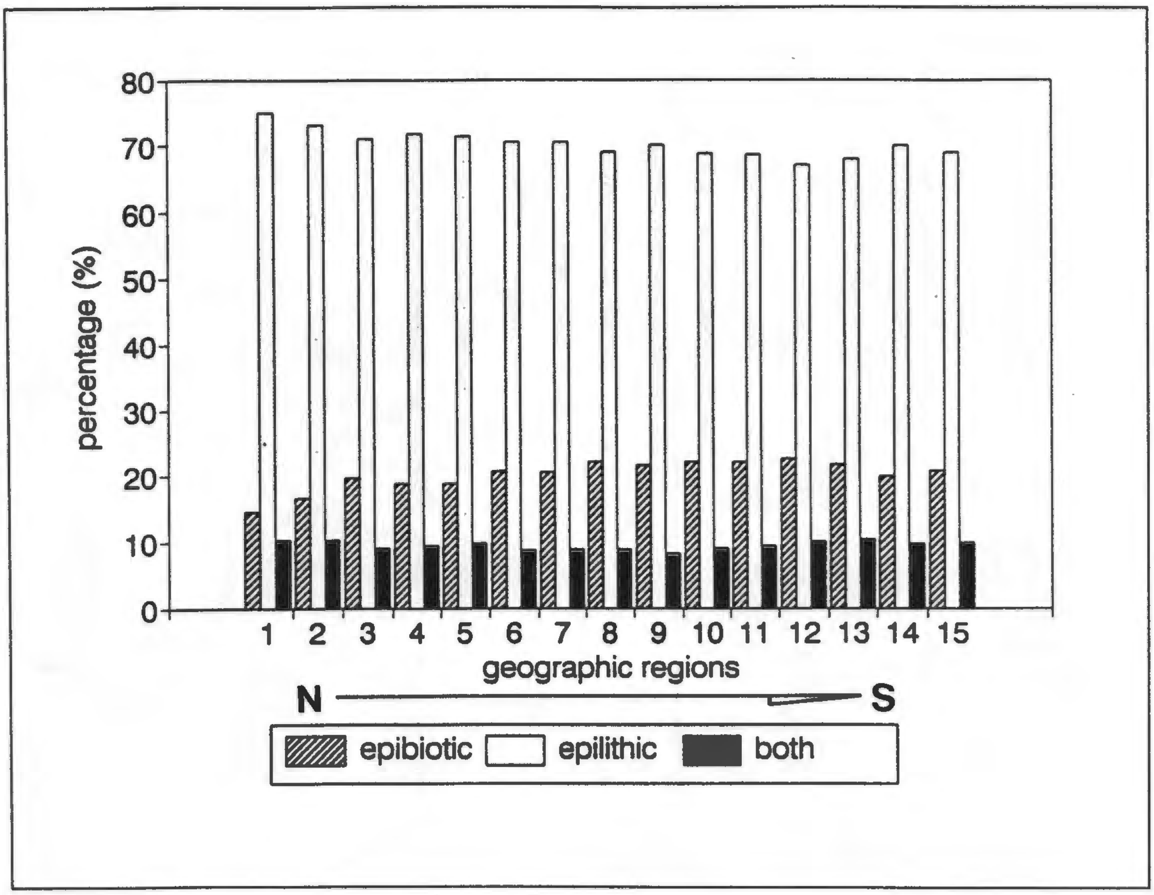

Fig 15 The percentage of species at each geographical region found growing on various substrates (for geographical regions see table 1).

Between the divisions the percentages of epibiotic, epilithic species, and those found on both substratum types remains fairly constant, following the general pattern with the majority of species being epilithic, followed by epibiotic species, with the fewest found on both substratum types. The one break in the pattern being the reds which have almost twice as many epibiotic species as the browns, and three times as many as the greens (see table 5).

Table 5 The percentages of each division comprised of epibiotic, epilithic or species found on both substrate types.

Division	Epilithic %	Epibiotic %	Both %
Phaeophyta	75.5	17	7.5
Chlorophyta	85	10	5
Rhodophyta	62	30	8

There is a decrease in the number of epilithic species with a vertical progression down the shore, accounting for 100 % of the substrate preference in the supralittoral (zone 1), and 60% in the deep sub-littoral (zone 7). The number of epibiotic species increases to around 35% in the deep sublittoral. Those found on both substratum types peaks at the mid-eulittoral, at just above 10% of the flora, and declines steadily thereafter (see fig 16).

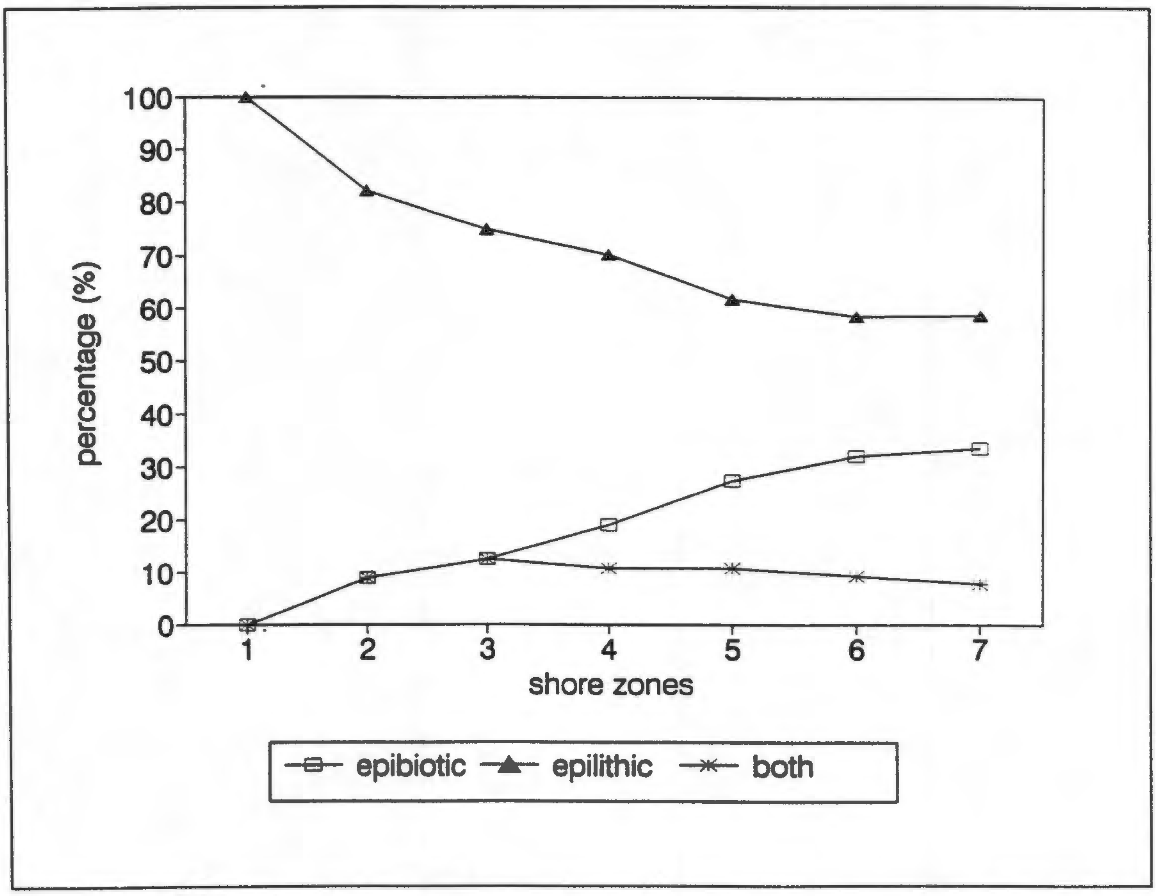

Fig 16 The percentage of species attached to different substrata in each shore zone (for shore zone descriptions see table 2).

In the different shore pool zones the majority of the species are epilithic, and a similar increase in epibiotic species, with an increase with depth, as seen in the shore zones, is seen in the shore pools. Those species which are both epibiotic and epilithic decline gradually with a progression further down the shore. The epibiotic species show a peak in the upper eulittoral zone in the shore pool zones (see fig 17).

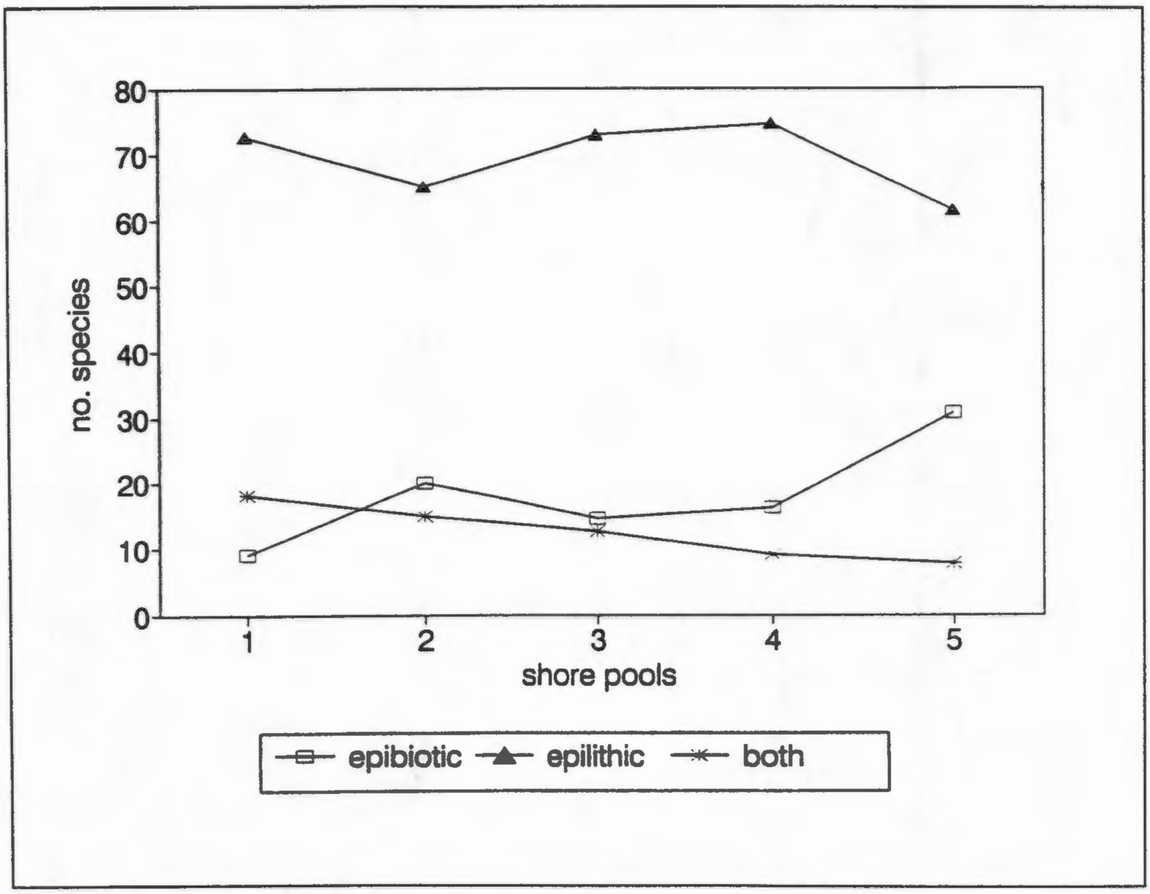

Fig 17 The percentage of species growing on each type of substrates in the different shore pool zones (for shore pool zone descriptions see table 3).

Discussion

Biogeographic distribution patterns

Beta diversity is described as the extent of species replacement along a gradient, indicating the degree by which habitats are partitioned by species (Wilson & Shmida 1984). The stretch of coastline reviewed in this study from southern Namibia and through the western overlap region is partitioned into two distinct communities of species (see fig 4). While at no point is there complete turn over along this coastline, a dramatic change in species composition is evident in the high beta diversity recorded around the Cape Peninsula (region 10). This same split is shown by the TWINSPAN analysis (see fig 6), where two distinct suites of species are evident to either side of Cape Point. At Cape Point we see the termination of the Benguela Province proper and the onset of the western overlap region.

The western overlap region from Cape Point to Cape Agulhas is the most diverse area in terms of species composition (see table 3). The intermediate temperatures of this region may allow for the presence of both warm-temperate species and cool-temperate species. This is apparent in the large number of species being lost and gained throughout the western overlap region (see fig 5). From as far north as Yzerfontein (region 7) there are a considerable number of species gained, and this number continues to increase around the coast to the east, with a peak in gained species at Cape Point, between Scarborough and Smitswinkelbaai (region 10). There is a similar decline in species in the opposite direction, though less dramatic in view of the increase in total species numbers with an easterly progression (see fig 5). In view of the high number of species gained around this region, it would appear that there is a considerable overlap of what may be warm-temperate species into the Benguela province. This is contrary to original beliefs, though based largely on marine fauna, where cool-temperate species were believed to extend further into the warm-temperate province (Lawson *et al.* 1991). This large gain in species from north of the western overlap region, combined with a loss of species with the onset of the western overlap region would indicate that this pattern does not hold for the seaweeds. There appears rather to be a considerable area of overlap, with many warm-temperate species found as far north as Yzerfontein (region 7) on the west coast.

The high diversity of the False Bay region may be attributed to its biogeographic position, situated as it is between two marine provinces (Bolton & Anderson in press). This may allow for a greater number of typically warm-temperate species to be present in this region, while still maintaining cool-temperate species such as *Botryoglossum platycarpum*, *Enteromorpha linza* and *Laminaria pallida*, whose ranges extend into the start of the western overlap, but go no further. There is also the fact that this area has undoubtedly been more extensively collected than other areas in the study site In the view of the enormous number of undescribed species, may give a false appearance of diversity (Winston 1992). This is an unlikely explanation of patterns observed though, as it is more probable that the entire study area, as with the world at large, has been under collected (Norton *et al.* 1996). We may conclude that recorded species numbers throughout the whole region may not be a true reflection of the diversity of the area. While this will hopefully be remedied in the future, there are discernible biogeographic patterns in this study that clearly relate to environmental factors.

The most marked of these environmental factors denoting the biogeographic patterns of the area is sea water temperature regime. The TWINSPAN analysis (see fig 6) splits the western overlap region into two species communities. These are a False Bay area and the area to the east of False Bay from Cape Hangklip to Cape Agulhas. The False Bay area (regions 11 & 12) is the most species diverse area, possibly as a result of its experiencing more consistently warmer temperatures due to its isolated nature as a bay (Bolton 1986). As well as catering for a wide range of species, some species are restricted on this coastline to this small region, such as *Enteromorpha compressa*, *Bryopsis eckloniae* and an endemic, unidentified species of *Cladophora*. These types of distributions may be the result of more thorough collections at certain sites.

The west coast region from Scarborough to southern Namibia, recognised as a distinct species community by the TWINSPAN analysis (see fig 6) is also divided again into two dominant communities. These species communities being from Smitswinkelbaai to

Kommetjie, and from Melkbosstrand to southern Namibia. This division appears to be a function of the high number of species gained between Yzerfontein and Kommetjie (see fig 4 and fig 5), with few species being lost. This may relate to temperature, where possibly the upwelling regime is more extreme to the north of this area, restricting the presence of some warmer water species. The northern species community is yet again divided into two regions. These are from Yzerfontein to Lamberts Bay and from Hondeklipbaai to southern Namibia. This appears to be a function of species being gained. Lawson *et al.* (1991) describe the seaweeds of the southern Namibian coast as much like that of the South African west coast. They do make mention of the fact that Lüderitz is a bay, which may be an important factor in determining the seaweed composition of the area. Cool upwelling is particularly prevalent at Lüderitz, this combined with the high temperatures of the bay, with temperatures of as much as 21° C and occasional tongues of warm tropical water from the north, make this region unique with regards to temperature (Engeldow *et al.* 1992). The region from Yzerfontein to Lamberts Bay may also be a result of a different temperature regime. This area covers Saldanha Bay which, like the Lüderitz lagoon, though less extreme, experiences warmer temperatures than the surrounding area, with monthly mean temperatures of 18.3° C (Bolton 1986). Bay areas also experience less severe wave action, which may also contribute to the diversity and species composition of these areas.

It is interesting to note that while species composition changes, the ratios of reds, greens and browns throughout the study area are consistent with those of the other two South African marine provinces. The general pattern being that the reds account for roughly two thirds of the flora, while the greens and browns contribute a sixth each (see fig 3) (Bolton & Anderson in press). While there are more reds universally, this ratio does not appear to be a global pattern, making the consistency throughout this country interesting (Norton *et al.* 1996). A slight increase in the greens is evident between Saldanha Bay and Yzerfontein (region 6) and between Smitswinkelbaai to Muizenberg (region 11). This may relate to the sheltered nature of the bays, reducing wave action and maintaining higher temperatures. A further possible explanation is that it may relate to higher pollution levels characteristic of these bays (Wynberg 1993).

The decrease of species from south to north is difficult to explain, but follows a global pattern among the seaweeds (Lüning 1990; Bolton 1994). It is a pattern which has stimulated much debate as it contradicts the universal pattern of increased species diversity towards the tropics. Some arguments have been put forward to explain this anomaly. In this particular case the increase of sandy areas with a progression into Namibia, reducing suitable substrate for attachment, may be one explanation (Engledow *et al.* 1992; Bolton 1994). Another cause may be the upwelling regime, which is more extreme to the north and may account for the decline in species towards the equator (Bolton 1996). A pattern much the same as this occurs in southern Chile which has a similar environmental conditions and seaweed flora, which also decreases in diversity towards the north as upwelling becomes more extreme, and only those species tolerant of a wider range of temperatures will survive (Santelices 1980).

It is difficult to make global comparisons, where each study reviews such a specific area. The fact that this particular temperate region is different to other temperate regions has long been evident. This, among other things, is a function of latitude, being different to other temperate regions, and its unique temperature regime, resulting in its being called a cool-temperate region. It lacks the typical species composition of most Southern Hemisphere temperate regions. It lacks the brown species such as *Durvillaea* and *Lessonia* that generally characterise cold-temperate regions, but has other unique browns such as *Ecklonia maxima* (South 1979). The area most likely to display similarities is the coast of Chile, which is also a temperate region, experiencing similar upwelling and ENSO events. In comparison with Chile which has some 550 species, and is itself considered to be depauperate when compared to other regions such as California which has 668 species, the diversity of this stretch of the west coast of southern Africa can only be described as relatively poor (Norton *et al.* 1996). These global figures are given in figure 18 (Norton *et al.* 1996). However it must be noted that any global comparison of this magnitude is crude.

	C	P	R	Total
Pacific—Americas				
Arctic Pacific	12	30	38	80
S. Alaska–Oregon	117	143	373	633
California	72	137	459	668
Mexico	107	113	623	843
Peru	31	20	105	156
Chile				550
Tierra del Fuego				334
Pacific—Asia & Australasia				
Kurile Islands	31	71	83	185
Japan	235	376	899	1510
Korea	81	135	357	573
Tawain				490
Vietnam	115	86	223	424
Philippines	215	125	475	818
Northern Australia	189	149	374	713
Southern Australia	120	231	>357[1]	708+
New Zealand	96	138	383	617
Arctic Ocean	59	89	104	252
Antarctic Ocean				550
Atlantic—Americas				
Arctic Canada & W. Greenland	61	74	66	201
Newfoundland–N. Carolina	97	127	130	354
Cape Hatteras–Cape Canaveral	65	59	104	228
Florida & Dry Tortugas	133	61	227	354
Caribbean & adjacent waters	253	150	655	1058
Brazil	129	76	355	560
Argentina				*c.* 400
Atlantic—Europe & Africa				
N. Norway, Iceland, Spitzbergen, E. Greenland	67	101	112	280
W. Norway–Portugal	208	281	509	998
Mediterranean	214	265	*c.* 550	*c.* 830
Portugal–Morocco	91	114	355	560
Subtropical W Africa: Senegal–Mauretania	48	51	197	296
Tropical W Africa: Gambia–the equator	65	46	213	324
South Africa				*c.* 700

[1] Does not include Gracilariales, Bonnemaisoniales, Corallinales, and Rhodymeniales.

Fig 18 Global figures of seaweed diversity (Chlorophyta, Phaeophyta and Rhodophyta) (Norton *et al.* 1996).

The cool-temperate west coast has long been known to have a high number of endemics compared to other world regions (Bolton & Anderson in press). Endemism "hot spots" are described by Norton *et al.* (1996) as those areas where the endemics comprise more than 40% of the flora. The degree of endemism along this stretch of shore is very high (see fig 8). According to the above definition any one of the geographic regions considered could be termed a "hot spot" of endemism. At a global scale this portion of coast, with a total of 50.7% endemism, ranks very high and is comparable to regions like Antarctic and the Sub-Antarctic Islands. Again, it is important to consider the size of an area chosen for any study, where the incorporation of a larger geographic area may serve to reduce the total percentage of endemism.

The degree of endemism may not be related to the diversity of the flora, as is seen on the Pacific coast of South America, where the number of endemics remain constant along the stretch of the coast, while species numbers increase to the south, reducing the proportion of endemics (Norton *et al.* 1996). A similar pattern is apparent in this study, where though the total species curves, and that of the number of endemics follow each other fairly closely, the percentage of endemics of the total flora decreases with a southerly progression. In the Chilean case the pattern is accounted for with an increase in sub-Antarctic elements, which proportionally reduce the number of Chilean endemics (Santelices 1980). In this study, the combination of an increase in species numbers in all the divisions to the south, combined with the more variable climatic conditions experienced to the north make the pattern of reduced numbers of endemics to the south relatively easy to explain. This is not the case among the brown seaweed endemics, which follow a distinctly different pattern to that of the other divisions (Bolton 1996).

The brown endemics show a marked increase in percentage of their total diversity (see fig 8) with a southerly progression, in complete contrast to the patterns displayed by the reds and greens (see fig 8). This may be a function of variable histories of the different divisions. While the origins and distribution patterns of the South African reds have been well studied, less has been done on the greens and browns (Hommersand 1986), as a result no speculations can be made. Another possibility is that the particular temperature regime found in the south, being both less variable of that of the west coast, and yet cooler to that of the warm-temperate province, may account for these endemics. It is interesting to note that it was these species, such as kelps like the endemic *Ecklonia maxima*, which were looked to determine the temperature status of this coastline. The belief was that these kelps are characteristically cold temperate species, as has been demonstrated in the northern hemisphere. Many of the kelps found on this coast are found in warmer temperatures, indicating this coast not to be a cold temperate coast as previously supposed (Lawson *et al.* 1991).

The particular geological history of this coastline may have served to create this combination of low diversity and high endemism among this seaweed flora. This coastline was formed in the early Cretaceous, 120 - 130 million years ago, as Africa moved away from the Antarctic (Lüning 1990). The shallow divide between African and South America deepened 65 million years later, since when this coast has been isolated. This coastline is thousands of kilometres away from any similar temperate systems, and has been isolated for a long time, possibly explaining the high proportion of endemics (Bolton 1986).

Present conditions are also distinct in the form of characteristic upwelling which brings cold water to the surface causing dramatic temperature changes over a short period of time. Less frequent ENSO events act to suppress this upwelling, resulting in unusually high temperatures. These factors make this coast climatically unique, which simultaneously suppresses diversity, reducing the number of species able to immigrate into the region, and enhances the evolution of southern African endemics (Bolton 1996). The upwelling regime, though some 10 million years old, has been at its present capacity for only the last 2 - 3 million years (Bolton & Anderson in press). These factors create a variable and unique environment, which has long been isolated, but with relatively recently developed environmental conditions, and act to select for a distinct marine flora.

Shore habitat diversity

There is a dramatic change in the characteristics of the vertical shore zones as physical conditions change rapidly with increasing distance from the shore. The extreme upper habitat limits of the shore are set by desiccation tolerance, while lower down on the shore, where species numbers are higher, competition and predation become more important determining factors (Bolton & Anderson in press). Few species can handle desiccation, this being evident in the increase in species numbers with a progression down the shore (see figs 9 & 10). The reduction of species in the subtidal pools is likely to be because the concept of a subtidal pool is meaningless. This is demonstrated in the fact that in the equivalent shore zone species numbers continue to rise with a progression down the shore. Many of those factors that distinguish pools for the surrounding shore are lost once the pool is frequently submerged.

The number of endemics found in each shore and shore pool zone increases with the number of species (see fig 9 & 10). The proportion of endemics remains fairly constant in both shore and shore pool zones, contributing around a quarter to a third of the total flora. In the supralittoral though there are considerably less endemics, figure 11 shows that there is only one endemic in this zone, this is the red seaweed *Porphyra capensis*, which grows in this zone with non-endemic greens such as *Ulva capensis, Enteromorpha flexuosa* and *Enteromorpha intestinalis* (see fig 11). It may be that conditions in the eulittoral and supralittoral, though harsher, are more universal, and a few widespread species can survive. In contrast, the conditions off shore in the sub-littoral are more unique given the specific characteristics of this coast, this explaining the greater proportion of endemics.

The turnover of the divisions with a progression down the shore (see fig 11 &12) is possibly related to light. Light is an important factor determining vertical distribution, particularly of those of the subtidal zone where it becomes limiting. The two clear patterns evident from this data are the decrease in greens from the supralittoral down, and an increase in reds with progressively deeper water. Reds are tolerant of the low light conditions and found to dominate the intertidal on a world wide scale (Bolton & Anderson in press). The findings of this study are in agreement with Lüning (1990) who, in a general description of the vertical shore zones, describes the lower eulittoral as dominated by a belt of red algae. In this biogeographical study the dominance is continued down the shore into the deeper zones. The green algae are able to live at great depths, but only in clear waters which allow a large amount of light through. In the nutrient rich, and frequently turbulent waters of the west coast of South Africa this is however, not possible, and green algae, with their high light requirements are more abundant on the upper shore zones (see fig 13) (Lüning 1990).

Other important contributing factors to the vertical zonation patterns are biotic interactions, for example grazing and competition for space, and abiotic factors such as wave action. While desiccation is certainly an important factor, the few species in the upper and mid-eulittoral zones (zone 2 & 3) may be attributed, to some extent, to the competition, where seaweeds must compete for space with species of barnacles, such as of *Octomeris* (see fig 11) (Branch & Branch 1983). The slight reduction in green and brown seaweed in the subtidal fringe (zone 5) could be as a result of grazing by limpets such as *Patella cochlear*. Though why this would not affect the red seaweeds is not apparent.

This pattern could also be a function of wave action. Wave action serves to increase the height to which species can grow on the shore, and generally greater seaweed biomass is found on those shores which experience greater wave action (McQuaid 1985). Some species of seaweed are better adapted to wave action than others, and wave action will often serve to increase seaweed biomass, and not necessarily diversity. In this study, where the coastline has both exposed and sheltered shores, no direct reference can be made with regards to wave action in the vertical zonation patterns.

The patterns of epilithic, epibiotic and those species found on both substratum types are fairly consistent throughout the geographic regions (see fig 15). All three categories increasing with the increase in species numbers around the Cape Peninsula, but consistently higher numbers of epilithic species are maintained. There is a slight increase in the percentage of epibiotic species towards the Cape Peninsula and around the western overlap. Perhaps the increase in diversity gives greater scope for attachment, as many seaweed epiphytes are host specific (Lüning 1990). Sand inundated shores tend to show reduced species numbers. Engledow and Bolton (1994) found species numbers, within quadrats, to be reduced when sand cover was greater than 5.6 kg m^{-2}. It is interesting that the percentage of epilithic species is highest in region 1, in southern Namibia, where sand inundation would be expected to reduce available sites for attachment, and subsequently reduce the number of epilithic species. In region 1 in southern Namibia these epilithic species may be the turf-forming species which are common to this area (Engeldow *et al.* 1994).

There are more distinct patterns of substrate preference in the vertical shore zonation. With a progression down the shore there is an increase in the percentage of epibiotic species, and a decrease in epilithic species (see fig 16). This may correlate with the increase in the number of species further down the shore, allowing for more host species for epibiotic species to attach to. In the pools this change takes place faster which is not in response to an increase in the number of species with greater submersion as the upper eulittoral shore and shore pool zones have equivalent species numbers. This pattern corresponds with the increase in the number of Rhodophyta (see figs 13, 14 & 17), Rhodophyta having characteristically higher number of epibiotic species (see table 5). Lüning (1990) suggests epibiotic growth is also a way to increase proximity to light, where, by growing on another seaweed or animal, the organism may be bought closer to the light (Lüning 1990). This is demonstrated here with the increase in epiphytes with greater depth, and also the higher number of epiphytes in pools, which may be darker than the equivalent area on the shore. This pattern may also be in response to the high number of ephemeral species that grow in the higher regions of the shore, reducing the number of epiphytes which require a lasting thallus for attachment.

Conservation of our seaweed flora

Despite the ethical merit to the conservation of seaweeds in their own right, they also fulfil important ecological roles, and are thus vital to the health and persistence of rocky shores communities. Seaweeds play a dominant role in determining habitat structure and faunal composition and distribution. Seaweeds frequently act as nurseries for fish, which may be of conservation as well as economic significance (Norton *et al.* 1996). Changes in the oceans are characteristically slow and not of great amplitude, rendering organisms living in the sea potentially more vulnerable to any sudden change (Norton *et al.* 1996). Pollution has been shown to reduce seaweed diversity which can in turn result in disjunct populations, rendering more species vulnerable to extinction.

In South Africa pressure on the coastlines takes the form of mining, fishing, development and tourism. It is estimated that 470 000 tons of waste is discharged into our seas every year (Robinson & de Graaf 1994). The areas of greatest impact in the study area are believed to be Table Bay, False Bay and Saldanha Bay, where anthropogenic pressures are greatest (Wynberg 1993). This study however, fails to demonstrate any reduction in diversity here as a result of these impacts. Slight changes in species composition, such as the increase in greens seen around the False Bay and at Saldanha (see fig 3) may be evidence of the higher pollution status of these areas. Threats faced by our marine environment include the lack of any managerial co-ordination, environmental monitoring, and stringent legislation to secure the future existence of these communities (Wynberg 1993).

Hockey and Buxton (1989) demonstrate that only 9.5% of the approximate 3000 km coastline of South Africa is adequately conserved. Only 5.8% of the coast presently conserved is of rocky shore, where the vast majority of the seaweed species are found. While the document on marine protected areas in this country lists some 44 protected areas in the study site, the conservation status of these areas varies considerably (Robinson & de Graaf 1992). Of these 44 protected areas, the majority fall between Saldanha Bay and Cape Agulhas, with very few to the north west of this area, none of which are comprised of rocky shore (Emanuel 1992).

The uniqueness of the seaweed flora of the cool-temperate province is quite apparent, with both high levels of endemism and great beta diversity between some species communities. Our shores are more pristine than other, more developed countries. As yet we have no truly problematic invasive seaweeds, which may also stand testimony to the unique nature of our shore conditions (Robinson & de Graaf 1992). The threat of invasion and increased levels of pollution are ever present. Marine conservation in Africa is lacking, with South Africa as only one of four sub-Saharan countries to have any marine reserves (Hockey & Branch 1994). This combination of factors make it important to make sufficient arrangements for effective seaweed conservation soon.

To decide where the best areas for in situ conservation are, one must first decide the motivation for conservation. Emanuel *et al.* (1992) identify three main points for conservation. These are firstly for the conservation of species of interest, such as rare of endemic species. Secondly, conservation of entire functioning communities and finally for the maintenance of biotic diversity. The best way to achieve both these last two goals is to maintain coastal reserves covering a wide variety of habitats. Hockey and Branch (1994) developed a "middle and edge" policy to reserve sitings. According to this idea the best areas for conservation are those areas of high turnover, and the areas to each immediate side. In this way both representativeness (middle) and uniqeuness (edge) are conserved. Emanuel et al's (1992) species of interest would be those determining the edge, and biotic diversity would be those in the middle. In this study area three areas show high turnover (see fig 4) these being to the north in southern Namibia from Lüderitz to Port Nolloth, in the south west from Yzerfontien to Melkbosstrand and around the Peninsula in the False Bay region. An ideal strategy for the effective universal conservation of the seaweed of this coast would include a reserve on each turnover site, incorporating an area to the south east of each turnover site.

The Orange River Mouth Wetland Reserve is a national park that covers some of the area of the first site on the South African border. Although this area may conserve some seaweed species, there is often a reduction in seaweed diversity at river mouths as runoff from the land can make waters less saline, murky and warmer than normal (John 1994). South of Port Nolloth is the Mc Dougall Rock Lobster Sanctuary which, though not set out to conserve more than the rock lobster, may conserve some of the seaweeds of this area. While these two areas may conserve many turf-forming species found here, the majority of these conservation areas do not incorporate rocky shores. The development of a rocky shore reserve here is necessary. Much of this coastline was circumstantially conserved through the restriction of access to mining areas in the past. Now that many of these areas are being disbanded, there is a growing need for a reserve here (Emanuel 1992). This is presently the least protected area, and a reserve here would ensure the conservation of the southern African endemics found here, this northern area having a total of almost 60% endemism (see fig 8).

Around the Yzerfontein region there are several small reserves such as Dassen Island, Bokbaai Nature Reserve and Robbesteen. The presence of these reserves means that the only conservation requirement here is for a seaweed policy to be incorporated into the present management strategy of these reserves. The region around Cape Point and False Bay area has the most numerous reserves, including the Cape Point Nature Reserve which covers the largest protected area in the study area. Conservation objectives here serve to protect many of the brown seaweed endemics, which are prolific around the Cape, as well as the high diversity of this area. These present protected areas need to be expanded if they are to incorporate areas of edge and those in the middle of each community.

It is important to reiterate that Hockey and Buxton (1989) found only a small portion of the coast of this country to be adequately conserved. Although figures indicate the existence of a great number of reserves and protected areas along the coastline of this study area, the management of these areas may not be adequate for the conservation of the various seaweed species. This study has demonstrated that many endemics lie off the shore (see fig 9 & 10). The very specific nature of many of the protected areas in this country, such as for rock lobster conservation, means that often only specific vertical zones are conserved, and not the entire shore. For seaweed conservation to be effective the full extent of the shore must be conserved. Seaweeds have never formed a component of the criteria for the lay out of any reserve in this country. The management of each reserve along this coast needs to be investigated to determine whether an effective strategy for the conservation of seaweeds can be incorporated into their existing conservation policies.

Conclusion

The coastline from north of Lüderitz, to east of Cape Agulhas is indeed unique. Unusual present day climatic conditions combined with a unique geographic history make this flora different to that of other temperate areas. Despite its moderate levels of diversity the area has very high levels of seaweed endemism. This coastline also displays interesting patterns of endemism, with the browns displaying a different pattern to the other divisions. The coast also displays a high level of variety in having certainly two very distinct seaweed floras. These factors make seaweed conservation within the study area imperative. Despite the fact that there are numerous protected areas along the west and south coast of South Africa, none of the existing conservation areas were selected on the basis of seaweed conservation. While many of these areas may cover regions ideal for seaweed conservation, the policy of each protected area must be redressed so as to incorporate a strategy for the conservation of seaweeds. With this unique flora and a relatively pristine coastline, South Africa has a singular opportunity, and indeed responsibility to ensure the conservation of this seaweed flora.

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